

A *Dichocarpum*-like Angiosperm from the Early Cretaceous of China

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Abstract: The Yixian Formation (the Early Cretaceous) of China has yielded a diverse group of early angiosperms, revealing the charm of angiosperms from the formation is far from finishing. Here we report a fossil angiosperm, *Nothodichocarpum* gen. et sp. nov., with physically connected female parts, male parts, branches, and leaves with pinnate reticulate venation from the Yixian Formation of Liaoning, China. In addition to the previous reports, this report underscores the diversity of angiosperms in the Early Cretaceous Yixian Formation and earlier origin of angiosperms. The morphological variations in the reproductive parts in different stages allow us to infer the development of this early angiosperm. This fossil plant demonstrates a unique character assemblage that sheds new light on the origin and evolution of carpels.

Key words: angiosperm, *Nothodichocarpum*, Early Cretaceous, Liaoning, Yixian Formation

1 Introduction

Angiosperms are the most species-rich plant group in the world (Bell et al., 2010). Studies on angiosperms, especially their origin, evolution and systematics, have long attracted the attention of botanists over centuries. Molecular systematics, which is increasingly popular over the past two decades, has placed *Amborella* and *Nymphaeales* as the basalmost clades in angiosperms (Qiu et al., 1999; APG, 2009). In the meantime an increasing number of fossils from the Jurassic and Early Cretaceous have been interpreted as of angiosperms, including *Chaoyangia*, *Archaeofructus*, *Sinocarpus*, *Callianthus*, *Liaoningfructus*, and *Baicarpus* from Liaoning, China (Duan Shuying, 1998; Sun et al., 1998, 2002; Leng and Friis, 2003, 2006; Ji Qiang et al., 2004; Wang Xin and Zheng Shaolin, 2009; Wang Xin and Zheng Xiaoting, 2012; Wang, 2010a; Wang Xin and Han Gang 2011; Han Gang et al., 2013), *Schmeissneria* from northeastern China and southern Germany (Wang et al., 2007; Wang Xin, 2010b), and *Euanthus* and *Juraherba* from northeastern China (Liu and Wang, 2015; Han Gang et al., 2016), thus providing valuable data on the origin and early evolution

of angiosperms.

To enrich the existing knowledge pool on early angiosperms, here we report a new fossil plant *Nothodichocarpum* gen. et sp. nov., including female and male parts physically connected with leaves with pinnate reticulate venation recovered from the Yixian Formation. Characters of *Nothodichocarpum*, including decussate branching pattern, dorsal insertion of ovules, and combination of male and female parts, provide additional information on the diversity of Early Cretaceous angiosperms, and its parts preserved in different stages enable us to understand the development of this early angiosperm.

2 Materials and Methods

The Yixian Formation of Liaoning, China is well known for its vertebrate fossils (Teng et al. 2014) and early angiosperm fossils, including *Chaoyangia*, *Archaeofructus*, *Sinocarpus*, *Callianthus*, *Baicarpus*, and *Liaoningfructus* (Duan Shuying, 1998; Sun et al., 1998, 2001, 2002; Friis et al., 2003; Leng and Friis, 2003, 2006; Ji Qiang et al., 2004; Dilcher et al., 2007; Wang Xin and Zheng Shaolin, 2009; Wang Xin and Zheng Xiaoting,

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2012; Wang, 2010a; Wang Xin and Han Gang, 2011; Han Gang et al., 2013). In addition to Angiosperms, Bryophyta, Lycopodiales, Equisetales, Filicales, Pteridospermae, Cycadales, Bennettitales, Ginkgoales, Czekanowskiales, and Coniferales have been reported in the Yixian Flora (Wu Shunqing, 1999; Sun Ge et al., 2001; Zheng Shaolin et al., 2005). Together with abundant fossils of animals (including insects) (Wang Wuli et al., 1989; Wang Mei et al., 2009; Zheng Shaolin et al., 2005; Li and Luo, 2006; Liu Ming et al., 2006, 2007; Yao et al., 2006; Ren Dong et al., 2009, 2010; Shih et al., 2010; Gao et al., 2013), these fossils constitute the unique Jehol Biota, providing evidence and clues to the palaeoenvironment and palaeoecology involved in angiosperm evolution and diversification in the Early Cretaceous.

Previously, there used to be some controversy regarding the age of the Yixian Formation (Sun Ge et al., 1998, 2001, 2002; Swisher et al., 2002; Leng and Friis, 2003, 2006; Ji Qiang et al., 2004), but there is now a general consensus on the age of Yixian Formation, namely, approximately 125 Ma (the Barremian-Aptian, Early Cretaceous (Dilcher et al., 2007)).

The material of *Nothodichocarpum* gen. et sp. nov. includes a specimen preserved as compression/impression with some coalified residue. The specimen is 38 mm long and 21 mm wide preserved on a slightly yellowish gray siltstone slab approximately 11.5 cm x 12 cm. The slab was recovered from the Dawangzhangzi, Lingyuan, Liaoning, China (Fig. 1), the same locality as for *Sinocarpus decussatus* and *Archaeofructus sinensis*, by GH. The specimen was photographed using a Panasonic Lumix digital camera and a Nikon SMZ1500 stereomicroscope with a Nikon DS-Fi1 digital camera at the Nanjing Institute of Geology and Palaeontology (NIGPAS). Subsequently, a nitrocellulose replica of the specimen was made according to Zhu Weiqing (1983), and the replica was cleaned with HCl and HF, coated with gold, and observed using a Leo 1530 VP SEM (scanning electron microscope) at NIGPAS. Sketches were drawn from the pictures using Photoshop 4.0 by Ms. Lijun Chen. The specimen was deposited in the Palaeontological Center, Bohai University, Jinzhou, China.

3 Results

Nothodichocarpum gen. nov., Han et Wang

Type species: *Nothodichocarpum lingyuanensis* gen. et sp. nov., Han et Wang

Generic diagnosis: Distal portion of the plant including branches, leaves, and flowers. Branch slender, straight or slightly curving, with evident nodes. Branches axillary,

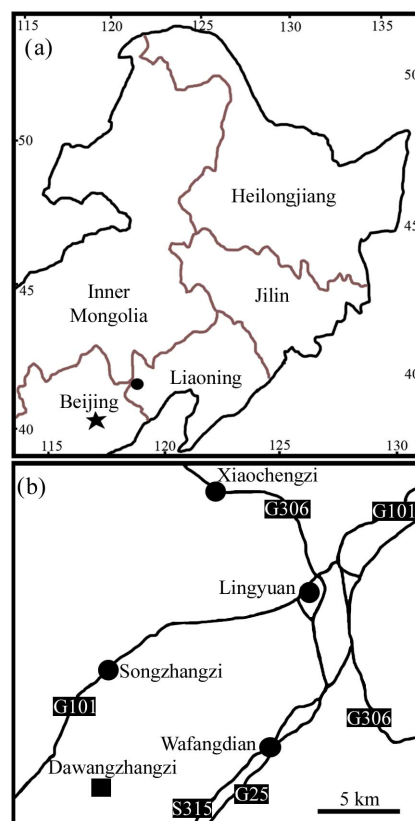


Fig. 1. Geographical position of the fossil locality for *Nothodichocarpum* in Liaoning, China. (a), Fossil locality (black dot) in northeastern China; (b), detailed position of fossil locality (black square) in suburb of city Lingyuan, Liaoning.

subtended by leaves. Leaf elongated oboval, petiolate, with pinnate reticulate venation and an attenuated tip. Petiole slender and straight, smoothly transitional to rigid midrib. Leaf margin with distantly spaced teeth. Both female and male parts present, lacking perianth. Male parts opposite or alternate with the carpels/follicles, composed of a slender filament and a long anther. Gynoecium composed of two divergent carpels. Each fruit lacking an obvious style. Fruit follicular, divergent, enclosing two rows of seeds inserted along the dorsal.

Etymology: *Notho*-, for false in Latin; *-dichocarpum*, for *Dichocarpum*, an extant genus in Ranunculaceae with superficial similarity to this fossil.

Nothodichocarpum lingyuanensis gen et sp. nov., Han et Wang
(Figs. 2–4)

Specific diagnosis: the same as the genus.

Description: The distal portion of the plant is preserved as compression/impression, 38 mm long and 21 mm wide (Figs. 2a, 4a). The specimen includes branches, leaves, flowers, and follicles (Figs. 2a, 4a). At the bottom there are two oppositely arranged leaves, and a branch is

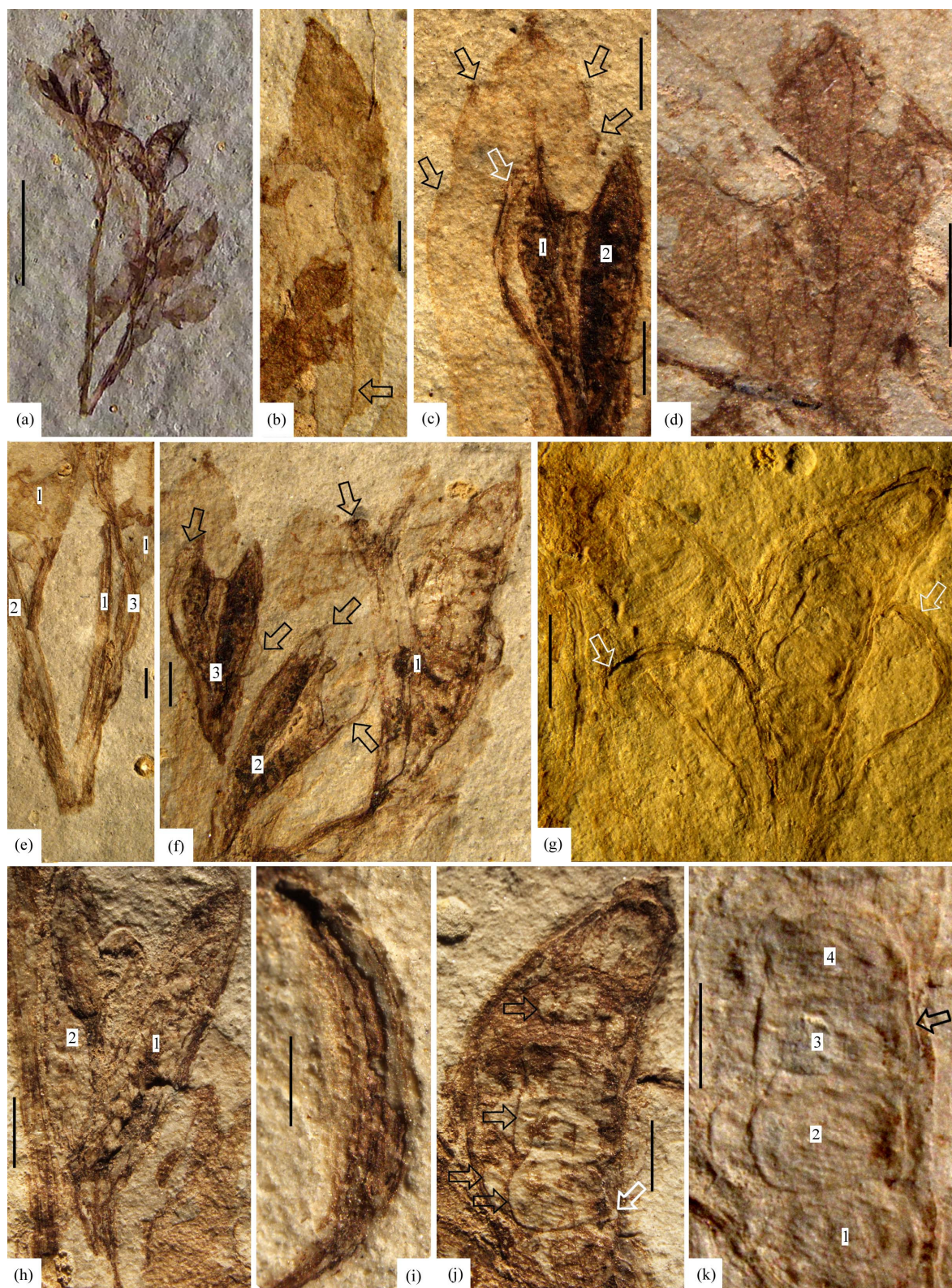


Fig. 2. Holotype of *Nothodichocarpum* and its details. HGP038.

(a), Holotype including branches, leaves, and flowers. Refer to Fig. 4a. Bar = 1 cm. (b), One of the leaves with a midrib (arrow). Bar = 1 mm. (c), Another narrow obovate leaf with attenuated tip and several teeth (black arrows), overlapped by a young flower including two carpels (1, 2) and at least one male part (white arrow). Bar = 1 mm. (d), Pinnate venation in one of the leaves. Bar = 0.5 mm. (e), Opposite branching. Note the main branch (2), axillary branch (1), subtending leaf (3), and leaves (1). Bar = 1 mm. (f), Three flowers (1-3) of different stages overlapping leaves. Note several male parts (arrows) beside carpels. Bar = 1 mm. (g), Two divergent, basally coalescent follicles and two male parts (arrows). Note the spatial relationship between the follicles and male parts. Bar = 2 mm. (h), Two young basally coalescent carpels (1-2). Bar = 1 mm. (i), Detailed view of the right male part in Fig. 2g. Bar = 0.5 mm. (j), The right fruit in Fig. 2g, showing abutting seeds (black arrows) inserted along the dorsal vein (white arrow). Bar = 1 mm. (k), Four abutting seeds (1-4) in the fruit shown in Fig. 2g. Note seed 4 is apparently connected to the dorsal of the fruit (black arrow). Bar = 1 mm.

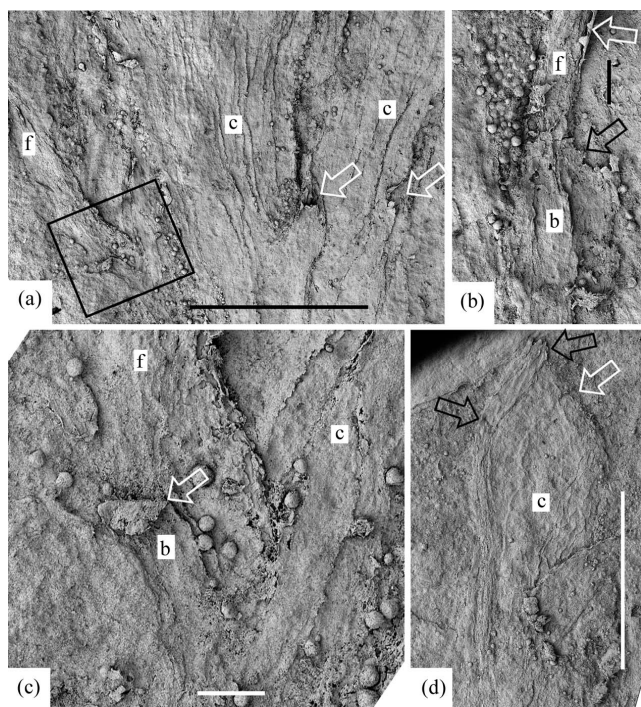


Fig. 3. Details of flowers under SEM.

(a), Basal portion of the fruit shown in Fig. 2g. Note the scars left by fallen off male parts (arrows), and their spatial relationship with the carpel (c) and filament (f). Bar = 1 mm. (b), A filament (f, white arrow) subtended by a bract (b, black arrow). This male part corresponds to the one marked by left white arrow in Fig. 3a. Bar = 0.1 mm. (c), Detailed view of rectangle in Fig. 3a. Note spatial relationship among the bract (b), filament (f) in its axil, and carpel (c). Bar = 0.1 mm. (d), Detailed view of the right follicle of fruit 2 in Fig. 2f. Note the relationship between the carpel (c, white arrow) and male part (black arrows). Bar = 1 mm.

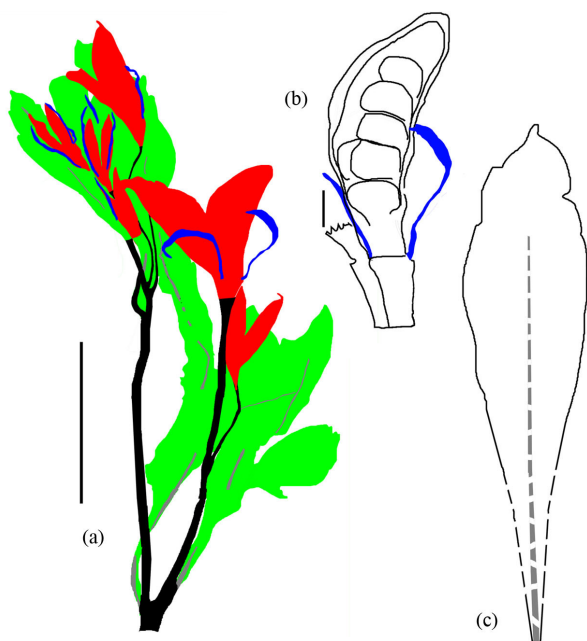


Fig. 4. Sketches of *Nothodichocarpum*.

(a), Sketch showing the physical connection among various parts. Green: leaf; gray: leaf vein; red: follicle/carpel; black: branch; blue: male part. Bar = 10 mm. (b), The fruit shown in Figs. 2g and 2j. Note the seeds inserted onto the dorsal vein (right) and male part (blue). Bar = 1 mm. (c), Semi-idealized sketch of the leaf shown in Fig. 2c.

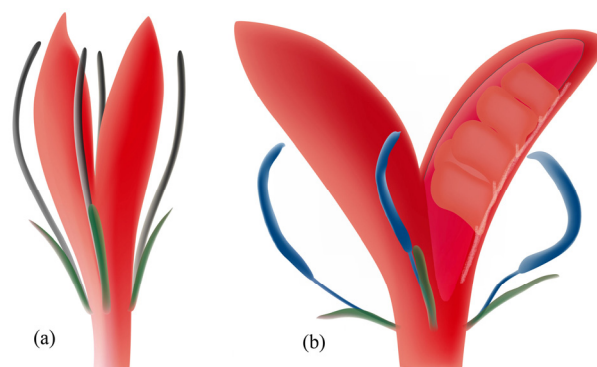


Fig. 5. Reconstruction of *Nothodichocarpum* in its flower (a) and fruit (b) stages. Note the dorsal vascular bundle connected with seeds in an opened fruit (b).

inserted in one of the leaf axils (Figs. 2a, 2e). Approximately 19 mm above this node there is another node, at which the same branching pattern is seen (Figs. 2a, 4a). The main branch is rigid, with fine longitudinal striations, slightly tapering distally, approximately 0.8 mm wide and wider than all other branches (Figs. 2a, 2e). The leaves at the bottommost node are larger than others in the same fossil, up to 22 mm long, with a strong petiole (Figs. 2a, 2e, 4c). The leaf at the node just above the bottommost one is smaller, approximately 17 mm long and 3.2 mm wide (Figs. 2a, 2c). The leaves are symmetrical, narrow obovate, with acute apex, decurrent acute base, and toothed margins (Figs. 2a-c). The teeth are sparse and more concentrated to the distal portion of the leaves (Figs. 2b-c). The midrib is moderate, slightly curving (Figs. 2b, 4c). The lateral veins form pinnate venation (Fig. 2d). Male and female parts are concentrated on the termini of the branches (Figs. 2a, 2c, 2f, 2g, 2h). The branch in the bottommost leaf axil gives rise to a flower in its middle, and is terminated by a pair of follicles (Figs. 2a, 2g, 2j-k). No perianth is seen (Figs. 2a, 2c, 2f-h). At least two male parts may be preserved (Figs. 2a, 2c, 2f, 2g, 3a, 4a-b). Some male parts are opposite the carpels, whereas others alternate with the carpels (Figs. 2a-c, 2f, 2g, 3a, 4a-b). Each male part may be subtended by a 0.26 mm wide strap-shaped bract, including a filament and an anther, both of which are relatively straight in the flower stage but become curving in the fruit stage (Figs. 3a-d, 4a-b, 5a-b). When mature, the filament is approximately 3.5 mm long and 0.1 mm wide, and the anther is approximately 2.2 mm long and 0.35 mm wide (Figs. 2g, 2i, 4a-b, 5a-b). Some of the male parts are appressed to the carpels initially but well separated from them when mature later (Figs. 2a, 2c, 2f-g, 3d, 4a). No *in situ* pollen grains are seen. The carpels are in pairs, in the center of the flowers, slightly coalescent at the bottom, divergent at the distal, without obvious styles, more or less lanceolate in shape, 4-8 mm long and

0.8–2.8 mm wide (Figs. 2a, 2c, 2f–h, 4a–b). Numerous ovules are present inside the carpels (Figs. 2c, 2f–g). Each follicle has a curving ventral side and more or less straight dorsal side, enclosing multiple seeds (Figs. 2a, 2g, 2j, 2k, 4a–b, 5a–b). The seeds are approximately 1.4 mm long and 1 mm wide, and arranged in two rows along the dorsal vein of the fruit (Figs. 2g, 2j, 2k, 4a–b, 5b).

Etymology: *lingyuan-*, for Lingyuan, the fossil locality.

Holotype: HGP038.

Type locality: Dawangzhangzi, Lingyuan, Liaoning, China (41°15'N, 119°15'E).

Stratigraphic horizon: the Yixian Formation, equivalent to the Barremian–Aptian, Lower Cretaceous (125 Ma).

Depository: the Palaeontological Center, Bohai University, Jinzhou, China.

Remarks: In the mature follicles of *Nothodichocarpum*, at most only two male parts are clearly seen (Fig. 2g), but the total number of male parts may be four. This possibility is suggested by the position of male part relative to the female part (Figs. 2g, 4a–b), e.g. one male part is opposite a follicle whereas the other is positioned between the two follicles. Furthermore, there are two scars (arrow in Fig. 3a) left by fallen-off parts, which are at the same level as the other male part and three of them are equal-distanced in Fig. 3a. Considering presence of two carpels, four male parts can be inferred for each flower of *Nothodichocarpum*.

The ovules/seeds of *Nothodichocarpum* have smooth intact margins on the ventral side, implying that they are not connected to the ventral margin of the follicles/carpels (Figs. 2g, 2j, 2k, 4b). This character is in agreement with the near-dorsal position of the seeds in the follicles (Fig. 2j, 2k, 4b), and there is some sign of ovule insertion on the dorsal side of the fruit (Fig. 2k). This positioning allows us to interpret the ovules as inserted on the dorsal margin of the follicle.

4 Discussions

Angiosperms are defined by the enclosed ovules and seeds, and are thus distinguished from other seed plants. Strictly speaking, only enclosed ovules before pollination can ensure an angiospermous affinity for a plant (Tomlinson and Takaso, 2002; Wang, 2010a). The seeds of *Nothodichocarpum* are apparently enclosed by the fruit wall, suggesting its angiospermous identity. This conclusion is further strengthened by the ovules enclosed in the young carpels, thank to the preservation of connected flowers and follicles in the same fossil. Both of these characters pin down the angiospermous affinity for

Nothodichocarpum.

The leaf morphology of *Nothodichocarpum* also provides important implication on its affinity. The leaves are oppositely arranged (Figs. 2a, 2e), unlike most basal angiosperms and monocots. Besides angiosperms, reticulate venation has been seen in other plants, including Gigantopteriales, Dipteridaceae, Glossopteridales, Caytoniales, and some Bennettitales (Harris, 1964, 1969; Sun Ge, 1981; Li et al., 1994). However, these alternative plants do not have enclosed ovules/seeds and thus have little to do with *Nothodichocarpum*. Thus the only alternative interpretation left for *Nothodichocarpum* is that it is an angiosperm.

There are several fossil and extant plants that share certain similar character assemblage with *Nothodichocarpum*. The gynoecium of *Callianthus* is characteristic of its two carpels, but *Callianthus* can be distinguished by its two characteristic divergent styles and its carpels surrounded by a fleshy layer (Wang Xin and Zheng Shaolin, 2009; Wang, 2010a). *Sinocarpus* may be the only one demonstrating by far the greatest resemblance to *Nothodichocarpum* in term of fruit morphology (Leng and Friis, 2003, 2006). However, the leaves of *Sinocarpus* require further effort to confirm, its male parts are missing, and its seeds are borne on the ventral side of the follicles (Leng and Friis, 2003, 2006). These factors prevent us from further comparison between *Sinocarpus* and *Nothodichocarpum*. Among the extant plants, *Dichocarpum* (Ranunculaceae) may be the one demonstrating the greatest similarity to *Nothodichocarpum*, in term of divergent follicles and pinnate leaf venation (Wu Zhengyi et al., 2001). However, the difference between these two genera are equally obvious, for examples, the ovules are inserted along the ventral side of the fruit in *Dichocarpum* but along the dorsal side in *Nothodichocarpum*, the teeth are far too weak in *Nothodichocarpum* than in *Dichocarpum*, and the perianth obvious in *Dichocarpum* is missing in *Nothodichocarpum*. These differences preclude further comparison.

The approximate arrangement of male and female parts in *Nothodichocarpum* (Figs. 2a, 2c, 2f–h, 3a, 4a–b, 5a–b) is a character noteworthy of consideration. Among seed plants, angiosperms are characterized by their flowers, in which male and female parts are frequently closely arranged. The unique feature of *Nothodichocarpum* is that each male part is subtended by a strap-shaped bract. This morphology is not frequently seen in other stamens of angiosperms, thus the male parts of *Nothodichocarpum* may not be fully homologous to stamens in other angiosperms. It appears that the whole male–female complex in *Nothodichocarpum* is an aggregation of male and female shoot systems, namely, the male part and its

subtending bract constitute a lateral complex, whereas the female part is the terminal shoot. Although such spatial arrangement of these parts is not completely in accordance with the conception of a flower, the possibility cannot be excluded that the aggregation of these two sexual shoots may have given rise to the angiosperm flower. Therefore, the closely arrangement of male and female parts in *Nothodichocarpum* is especially important for the derivation of the flower. If this aggregation scenario were true for flower-forming, then the assumed distinction between flowers and inflorescences would disappear: both are shoot systems with different degrees of aggregation, fusion, and reduction. However, this problem cannot be solved in the present study and requires further fossil evidence.

The dorsal insertion of ovules/seeds in *Nothodichocarpum* is a surprise and may shed some light on the origin of carpels in angiosperms. The ovules/seeds have been found inserted on the dorsal veins of the carpel wall in *Archaeofructus* (Ji Qiang et al., 2004; Wang Xin and Zheng Xiaoting, 2012). Parallel to this, *Nothodichocarpum* also has its ovules/seeds inserted on the dorsal vein of the carpel wall. To our knowledge, at least *Brasenia* (Cabombaceae) bears ovules inserted on the dorsal side of the carpel, forming contrast against many basal angiosperms with ovules inserted along the ventral side of the carpel (Eames, 1961; Endress, 2005). The latitude of ovule insertion in both early angiosperms and basal angiosperms suggests that the placenta in angiosperms is a part independent of the carpel wall and may freely fuse with the latter at any available point (Skinner et al., 2004). This conclusion is apparently against the Euanthium Theory, in which the ovules are assumed borne along the margins of the so-called megasporophylls (Arber and Parkin, 1907). Refuting Euanthium Theory is of significance in that this theory has been dominating angiosperm systematics in the past century.

The fossil of *Nothodichocarpum* has flowers/fruits preserved in different stages (Fig. 2a), allowing us to envision the development of the flowers/fruits. The male parts and carpels occur side by side in their early stage, but later, the male parts become curved and separated from the carpels/follicles. The most obvious change occurs in the gynoecium: the carpels in their early stage are lanceolate or linear, enclosing smaller ovules, and as the carpels develop into fruit, they become more inflated and divergent, convex on the ventral side and straight on the dorsal side, and enclosing much bigger seeds (Figs. 2c,f-h). The great change in the ovule/seed size implies that *Nothodichocarpum* invests little in its ovules and that the ovules may not develop until after pollination, a strategy

adopted by many angiosperms (Leslie and Boyce, 2012), in contrast to their gymnosperm peers (Ginkgoales and Cycadales) that frequently waste much energy and resources on big unfertilized ovules (Leslie and Boyce, 2012). It is very likely that such a strategy gives edges to angiosperms in their competition against gymnosperms.

Nothodichocarpum shares opposite phyllotaxy with basal angiosperms (including *Amborella* (Buzgo et al., 2004) and Chloranthaceae (Taylor and Hickey, 1996)) as well as early angiosperms (including *Chaoyangia* (Duan Shuying, 1998; Wang, 2010a), *Archaeofructus* (Wang Xin and Zheng Xiaoting, 2012), and *Sinocarpus* (Leng and Friis, 2003, 2006)). *Amborella*, the currently basalmost angiosperm (APG, 2009), has a decussate arrangement in its early development (Buzgo et al., 2004). *Chaoyangia* is proven a monoecious tricarpaceous angiosperm producing monocolpate pollen grains (Duan Shuying, 1998; Wang, 2010a), but it is frequently wronged as Gnetales due to its decussate branching pattern. Recent re-examinations of *Archaeofructus* indicated that this early angiosperm also has a whorled or at least opposite arrangement of follicles/carpels (Sun et al., 2002; Wang Xin and Zheng Xiaoting, 2012). Apparently, opposite/decussate branching pattern is a character shared by early angiosperms (*Nothodichocarpum*, *Chaoyangia*, *Sinocarpus*, and *Archaeofructus*) as well as basalmost angiosperm (*Amborella*), implying that such a branching pattern may be ancestral in angiosperms, not idiosyncratic of Gnetales as assumed previously.

5 Conclusion

Nothodichocarpum is an element of quite diversified angiosperms in the Yixian Formation. Its dorsal ovule insertion in the carpel implying that the carpels in angiosperms are not derived as assumed in the prevailing Euanthium Theory and decussate branching pattern shared among early angiosperms and basalmost extant angiosperm reminds botanists to re-evaluate the taxonomic value of this character with caution in their future practice.

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